Research Article

Horseshoe Crab Eggs Determine Red Knot Distribution in Delaware Bay

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Abstract

A decline in red knots (Calidris canutus rufa) has been attributed to horseshoe crab (Limulus polyphemus) egg shortages on the Delaware Bay, an important foraging area for migrating knots. We studied the movements and distribution of 65 radiotagged red knots on Delaware Bay from May to June 2004 and related movements to the distribution and abundance of horseshoe crab eggs and other prey and to other habitat characteristics. The number of horseshoe crab eggs was the most important factor determining the use of Delaware Bay beaches by red knots (logistic regression cumulative Akaike's Information Criterion adjusted for small sample size [AIC_c] $w = 0.99$). The knots shifted from emergent marsh and peat-beaches to sandy Delaware Bay beach when crab eggs became abundant, which also suggested the importance of crab eggs. While red knots used sandy beach zones more than expected, given their availability, 44% of red knot low tide locations were in bay and coastal emergent marsh. The abundance of Donax variabilis (AIC_c $w = 0.95$) and Mytilus edulis (AIC_c $w = 0.94$) spat, both food for red knots, had a relationship with red knot use of sandy beaches. Levels of disturbance and the abundance of laughing gulls (Larus atricilla) also were important factors in red knot sandy beach use, although secondary to prey resources (AIC_c $w < 0.4$). These results are consistent with the hypothesis that the abundance of horseshoe crab eggs on sandy beaches is driving movement and distribution of red knots and that there is little alternative food during the migratory stopover in Delaware Bay. Our findings that red knots disproportionately use Delaware Bay sites with abundant eggs and that there is a lack of surplus eggs at areas used and unused by red knots support the continuation of management for sustained yield of horseshoe crabs and other food resources at this stopover. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1704–1710; 2006)

Key words

The spring arrival of red knots (*Calidris canutus rufa*) at the Delaware Bay coincides with the largest spawning of horseshoe crabs (*Limulus polyphemus*) on the United States Atlantic Coast (Clark et al. 1993, Walls et al. 2002). Horseshoe crab eggs historically provided these birds with a reliable, abundant food supply (Wander and Dunne 1981, Shuster and Botton 1985). Red knots arrive at Delaware Bay with little body fat and often double their weight during the short 3-week stopover while feeding primarily on horseshoe crab eggs (Tsipoura and Burger 1999, Harrington 2001, Haramis 2003). Deposited fat must fuel the knots' migration to the Arctic breeding grounds and often must sustain them a week or longer while they await snowmelt (Morrison and Hobson 2004).

The *rufa* population of red knots has declined substantially in the past 2 decades (Morrison et al. 2004). During this period, a decreasing proportion of red knots has reached the weight required to complete the northward migration from Delaware Bay (Baker et al. 2004), and there has been mounting concern that horseshoe crabs have been over-exploited for bait and biomedical uses (Berkson and Shuster

1999, ASMFC 2004). One hypothesis attributes the knots' reduced weight gain and population decline to declining availability of horseshoe crab eggs in the Delaware Bay (Baker et al. 2004, Morrison et al. 2004).

If horseshoe crab egg availability is limiting weight gain, survival, and reproduction by red knots, then knots should disproportionately use sites with abundant eggs. If horseshoe crab egg availability is not limiting to red knots, then surplus eggs should be evident at areas used by knots, at areas unused by knots, or at both. We radiotracked red knots on Delaware Bay to determine if knot-used areas were richer in horseshoe crab eggs than other areas. We examined whether knots shifted from marshes to crab spawning beaches when the crab spawn peaked. We compared horseshoe crab egg abundance at knot-used and random areas to determine if egg abundance predicted the presence of knots. We sampled other potential prey species and habitat variables to control for alternate explanations for red knot distribution.

Study Area

Our study area was the Delaware Bay and Atlantic Ocean beaches and estuaries in Delaware and New Jersey, USA.

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The region contained wide to narrow sandy beaches, peat beaches, mudflats, creeks, tidal *Spartina alterniflora* and *S. patens* marshes, agricultural land, and residential developments. Relative habitat availability varied greatly over the tidal cycle (Burger et al. 1977).

We captured red knots in Delaware Bay in May 2004 with cannon nets on 5 beaches in New Jersey (Reed's Beach, Fortescue Beach, Kimbles Beach, Gandy's Beach, Rutger's Biological Station Beach) and 3 beaches in Delaware (Mispillion Harbor, Port Mahon, and South Bowers Beach). We distributed capture locations and applications of radiotags evenly around Delaware Bay, which is about 50 km long and 50 km across at its widest point.

Methods

Field Methods

We placed radiotags (Holohil Model # PD-2, Carp, Ontario, Canada) on a random sample of birds from each capture. Transmitter weight was <3.0% of body weight. We conducted daily aerial surveys of the entire Delaware Bay coastline and the Atlantic Ocean marshes and beach from Cape May, New Jersey, to Corson's Inlet, New Jersey, in a Cessna 172 aircraft. We systematically varied the tide state and the direction of the flight path. Transmitter range was 1,100 m from the aircraft at 300 m. Sixteen of 65 tags dropped from red knots during the study. We excluded from analyses all but the first locations of those tags at the drop sites. The birds lost the dropped tags 6–18 days after capture ($\bar{x} = 13.8$ d from attachment to loss).

Daily, we relocated a sample of radiotagged birds on the ground for behavioral, prey, and habitat sampling. We selected radiotagged birds according to a simple random sample, without replacement, of birds located during daily aerial and ground telemetry surveys. We prioritized the sampling of birds that had the longest unsampled time. The interval between sampling individual radiotagged knots was 1–14 days ($\bar{x} = 3.6$-d sampling interval) with this design. When we approached a radiotagged bird, we attempted to observe it. If we could not distinguish it from other flock members, we selected a focal red knot from the flock as close as possible to the apparent location of the tagged bird. We recorded the number of birds in the flock, species composition, and the extent (m^2) of the flock. We noted the focal bird's distance to the tide line, the tidal state (hour after high tide), the distance to and type of any potential disturbers within 200 m of the focal knot (dogs, predators, people to nearest 5 m), the number of spawning crabs within 50 m of the flock, and the general flock behavior (foraging, roosting). We collected 3 sediment core samples (10.5-cm diam, 3.5 cm deep) centered on the location of the focal knot and spread evenly across the estimated flock width, perpendicular to the tide line.

We collected similar data at randomly selected locations without red knots. We paired the habitat for each random point with the same habitat type of each sampled bird, but we limited the selection of the simple random point to the area of a 7.5′ United States Geological Survey quadrangle

sheet of the area of the sampled bird. We used regression analyses only to compare Delaware Bay beach radiotagged birds ($n = 51$) to Delaware Bay beach random points due to the low numbers of birds feeding on peat outcrops ($n = 11$) or in emergent marsh ($n = 6$). We did not observe birds on Atlantic Ocean beaches, so we did not collect random points from ocean beaches. At each random point, we collected 3 core samples spaced 5 m apart in a line perpendicular to the tide line and centered at the random point. If knots were present at the randomly selected locations, we collected behavioral and ecological data but did not use the data as part of the unused or used area random samples. We proceeded to other randomly chosen beach points until we found one without knots.

We preserved core samples in 95% ethanol. In the lab, we separated eggs and invertebrates from sand and other inorganic material by elutriation and flushing with water through a series of screens. We counted eggs and invertebrates in all samples and recorded dry weight for each prey type (crab eggs, *Donax variabilis*, *Mytilus edulis*, insect larvae, Polychaetes) in each core sample. We used the mean prey counts from all 3 samples at each location in regression analyses.

Data Analyses

We selected variables for regression analyses based on a lack of significant correlation with other variables, a univariate test P value < 0.50, or a hypothesized biologic importance to the birds during migratory stopover (Hosmer and Lemeshow 1989). We used these variables and their interactions to construct a global model (all selected variables and their interactions), a null model (intercept only), and 38 additional candidate models with varying main effects for Delaware Bay beach locations and random points. We used Akaike's Information Criterion with a small sample bias correction (AIC_c) to select the most parsimonious models (Burnham and Anderson 1998). We considered all models within 2 units of the minimum AIC_c model valid (Burnham and Anderson 1998) and we used them to make inferences from the model. We calculated AIC_c weights for each model and then calculated cumulative AIC_c weights for each variable by summing the AIC_c model weights of every model containing a given variable. Researchers can use AIC_c weights to contrast relative support for each model and variable (Burnham and Anderson 1998). We conducted model fit diagnostics for models selected by AIC_c including explorations of deviance, Pearson and Deviance residuals, likelihood ratios, and the Hosmer–Lemeshow test for goodness-of-fit (Hosmer and Lemeshow 1989, Fox 1991). We assessed multicollinearity through examination of variance inflation factors (VIF), condition indices, and variance-decomposition proportions (Belsley et al. 1980). We used likelihood ratios to further explore the contribution of each parameter to the selected models (Hosmer and Lemeshow 1989). We tested the accuracy of model predictions on data collected on non-radiotagged red knots sampled opportunistically on sandy Delaware Bay beaches during the study.

We reported the results of logistic regression modeling as the number of crab eggs per square meter of beach 5 cm deep to be comparable to data contained in management plans for Delaware Bay. Our reporting of eggs per square meter is scaled up from the number of eggs in a 3.5-cm-deep core with a surface diameter of 10.5 cm, assuming uniform distribution of eggs in the top 5 cm of sand.

Results

Landscape-Level Movements

We radiotagged 65 red knots comprised of 1–10 birds in 13 capture flocks. We relocated 64 individual knots in 249 relocations on 18 flights from 12 May 2004 to 4 June 2004. Due to migratory departures and temporal spacing of tagging activities, we relocated 2–44 birds ($\bar{x} = 20.9$) per aerial survey. Spatial analyses indicated that radiotagged birds captured as flocks intermixed with the larger radiotagged population and moved independently of capture flock members within 1 day of capture (S. M. Karpanty, Virginia Polytechnic Institute, unpublished data).

Red knots predominantly used sandy Delaware Bay beaches before and after the peak in crab spawning (Table 1). However, many bird locations (34% at high tide, Fig. 1A; 44% at low tide, Fig. 1B) were in other habitats. Knots in Delaware Bay emergent marsh were 100–3,860 m from sandy beaches ($\bar{x} = 1,310$ m, $n = 40$). We found knots in 10 different emergent marsh locations during high tide flights and 11 locations at low tide. Birds on peat beaches ($n = 29$) averaged less than 400 m from the water line. No red knots were located on Atlantic Ocean beaches in aerial or ground surveys; we excluded this habitat from further analyses. Proportional use of habitats before and after the peak in crab spawning was similar at high tide locations (Fig. 1A; $\chi^2_3 = 3.14$, $P = 0.37$), but there was more use of sandy beach (0.35–0.58 pre–post spawn proportion of sandy beach locations) and less use of peat beaches (0.35–0.09 pre–post spawn proportion of peat beach locations) after the peak in crab spawning activities at low tide (Fig. 1B; $\chi^2_3 = 9.30$, $P = 0.03$).

Selection of Delaware Bay Beaches

Crab eggs accounted for 91% of the biomass of potential prey items at knot-used sites and 94% at random sites, but the crab egg biomass at knot-used sites was >3.5 times larger than the egg biomass at random sites (Table 2; knot-used sites, $\bar{x} = 0.44$ g dry mass, $n = 51$, SE = 0.15; random, unused sites, $\bar{x} = 0.12$ g dry mass, $n = 54$, SE = 0.03). Biomass of other prey items at knot-used and random sites was small in comparison to crab eggs (D. variabilis, knot-used sites, $\bar{x} = 0.037$ g dry mass, $n = 51$, SE = 0.035; random, unused sites, $\bar{x} = 0.0022$ g dry mass, $n = 54$, SE = 0.0010; all other prey, $\bar{x} < 0.003$ g dry mass per sample).

Four of 40 candidate models describing red knot presence or absence from Delaware Bay beaches were within 2 units of the minimum AIC$_c$ value (Table 3). We examined deviance and Pearson residuals and DFBETAS and found no outliers in the models. We found no evidence of multicollinearity between model variables with the values of all VIFs <1.01 and no condition indices >5.

The most important variable in all models was the number of horseshoe crab eggs ($w = 0.99$), followed by the number of D. variabilis ($w = 0.95$, Table 3). We confirmed these results by examining likelihood ratios before and after removing various components of Model 1, the prey-only model. We reduced model fit by removing crab eggs and all associated interactions ($\chi^2_2 = 15.72$, $P < 0.001$), Donax and associated interactions ($\chi^2_3 = 11.71$, $P = 0.008$), Mytilus spat and associated interactions ($\chi^2_3 = 9.60$, $P = 0.02$), and the Donax × crab egg interaction alone ($\chi^2_4 = 10.15$, $P = 0.04$). The negative effect of disturbance ($w_i = 0.38$) and the positive effect of laughing gulls (Larus atricilla, $w_i = 0.38$, Table 3) on the model had less weight than food.

Model Validation and Inference

Logistic regression model predictions for randomly located, nontagged knots were similar to the predictions the models produced for sites occupied by the radiotagged knots which were used to fit the model (nontagged knots $\bar{x} = 0.59$, radiotagged knots $\bar{x} = 0.61$, Table 4). Predicted probabilities for nontagged knots were significantly higher than for the random points with no knots (random points $\bar{x} = 0.42$, Table 4).

Coefficient estimates for the number of crab eggs were stable between the 4 selected models (Table 3). We used Model 1, the best AIC$_c$-selected and most parsimonious model, to predict that in the absence of other variables, there must be ≥20,873 crab eggs/m² of beach to have a 50% chance of finding knots at a sandy beach site. Close to 252,942 crab eggs/m² are needed to have an approximately 99% chance of finding red knots at a sandy beach site (Table 5). Only 20% of all random point samples had enough crab eggs to have a predicted probability of red knots >50% (Table 5). Congruently, 8 of 51 initial random point beach samples (16%) harbored red knots and forced us to move on to additionally selected random points.

Discussion

Our random Delaware Bay beach locations suggest that a small portion of the bay shoreline (approx. 20%) contained enough eggs to have a >50% chance of finding red knots. Our discovery of knots at 16% of random beach locations suggests that knots attended most or all of the available egg concentrations. The selection of beaches with large numbers of horseshoe crab eggs and the shift from other habitats toward crab spawning beaches are consistent with the idea that horseshoe crab eggs are a key resource for red knots.

Whereas horseshoe crab eggs are the predominant red knot food in Delaware Bay (Tsipoura and Burger 1999, Haramis 2003), elsewhere along the migration route and on the wintering grounds red knots feed primarily on mollusks and bivalves (Gonzalez et al. 1996, Truitt et al. 2001). We observed red knots feeding primarily on horseshoe crab eggs but also on Donax and Mytilus spat and on Polychaetes.

Neither Donax nor Mytilus were significant predictors of red knot distribution alone, but in combination with

Table 1. Observed habitat use (no. locations[a]) by red knots and expected habitat use if knots were using habitat according to availability in Delaware Bay region, USA, May and June 2004.

Habitat zone	Total area (ha)	Proportion of total area (ha)	All locations[b]		Prepeak spawn[c]		Postpeak spawn[d]		
			Observed	Expected	Observed	Expected	Observed	Expected	
Sandy Delaware Bay beach	272	0.0126	151	3.14	32	0.62	119	2.52	selected
Atlantic coastal marsh	5,150	0.2391	29	59.51	5	11.71	24	47.8	avoided
Bay marsh/peat beach[e]	16,116	0.7483	69	186.25	12	36.65	57	149.6	avoided

[a] We recorded habitat use data from aerial telemetry flights over bay beach, Atlantic coastal marsh, Atlantic Ocean, and bay emergent marsh and peat beach habitats at both high and low tides. We conducted use-availability analyses by tide on all locations, prepeak spawn locations only, and postpeak spawn locations only. We excluded ocean beach from these analyses as no birds were relocated in this habitat.

[b] All locations, df = 2, $\chi^2 = 7058$, $P < 0.001$; high tide all locations $\chi_2^2 = 4126$, $P < 0.001$; low tide all locations $\chi_2^2 = 2986$, $P < 0.001$.

[c] Prepeak spawn, df = 2, $\chi^2 = 1616$, $P < 0.001$; high tide prepeak spawn $\chi_2^2 = 1620$, $P < 0.001$; low tide prepeak spawn $\chi_2^2 = 134$, $P < 0.001$. The peak in crab spawning was 19 May 2004.

[d] Postpeak spawn, df = 2, $\chi^2 = 5453$, $P < 0.001$; high tide postpeak spawn $\chi_2^2 = 2557$, $P < 0.001$; low tide postpeak spawn $\chi_2^2 = 2902$, $P < 0.001$.

[e] We combined Delaware Bay emergent marsh and Delaware Bay peat outcrops/beach in use-availability analyses because land use–land cover classifications do not distinguish these 2 habitat zones.
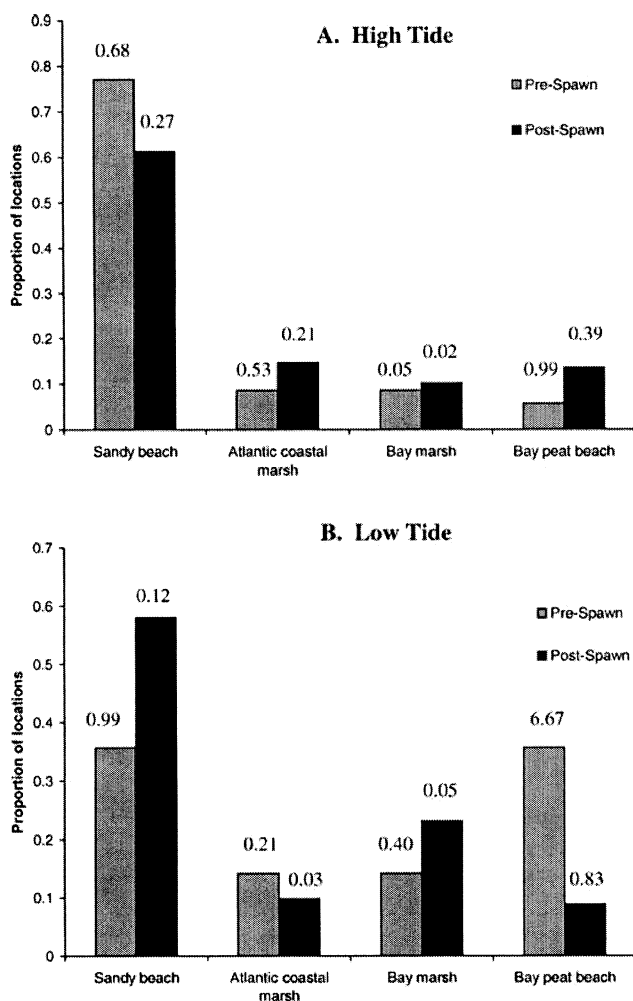

Figure 1. The proportion of aerial telemetry locations of red knots in four habitat zones, before and after the peak in horseshoe crab spawning activity, for high tide observations (A) and low tide observations (B), Delaware Bay region, USA, May to June 2004. The proportion of birds in sandy bay beaches was greater after the horseshoe crab spawn at low tide ($\chi_3^2 = 9.30$, $P = 0.03$) but not at high tide ($\chi_3^2 = 3.14$, $P = 0.37$). Partial χ^2 values are above each bar for the contribution of each proportion to the overall test statistic.

horseshoe crab eggs, they provide the best explanation of bird distribution. *Donax variabilis* most commonly occupy sandy beach zones of high salinity in Delaware Bay, whereas *M. edulis* spat may colonize a diversity of habitat types but most often settle in the soft sediments or seaweed beds more common in marsh and peat zones in the bay (Maas Geesteranus 1942, Donoghue 1999, Hyland et al. 2004). The negative parameter estimate of *Mytilus* is likely a habitat correlate related to its likelihood of settling in marsh or on peat beach, rather than a true negative relationship. Similarly, the negative parameter estimate for the interaction of *Donax* and crab eggs is likely an artifact of the patchy distribution of *Donax* in comparison to crab eggs and the discovery of a few red knot locations with large numbers of *Donax* but few crab eggs. While these non-egg prey do not obtain adequate densities or biomass on sandy beaches to support the large numbers of migratory shorebirds in comparison to horseshoe crab eggs, their presence with crab eggs is important to best determine the distribution of red knots on Delaware Bay.

Potential disturbance reduced the probability of finding knots on Delaware Bay beaches. In addition to observing disturbance of shorebirds on beaches open to public use, we saw many disturbance events on beaches already closed to public use with the intention of protecting shorebirds during the peak migration period. While we found the effect of disturbance to be secondary to the influences of prey resources, the negative effects of human disturbance and the presence of dogs near migratory shorebirds is well documented (Burger 1981, Burger and Gochfeld 1991). The positive relationship between laughing gull numbers and red knot presence is likely due to the use by both bird species of the sandy beach areas with the highest densities of horseshoe crab eggs for foraging. Burger et al. (2003) found evidence of a negative interaction mediated by interference competition between shorebirds and gulls feeding on crab eggs.

Management Implications

Horseshoe crab eggs dominated the biomass of potential prey items on Delaware Bay beaches. If crab egg numbers

Table 2. Mean, standard error, and test of the abundance of prey items and other variables at bay beach sites ($n = 51$) used by radiotagged red knots and random bay beach sites ($n = 54$) not used by knots in Delaware Bay, USA, May and June 2004.

Main effect variables	Red knot		Random point			
	$\bar{x}$	SE	$\bar{x}$	SE	T^a	P
Horseshoe crab eggs	303.98	101.47	86.13	19.99	−2.11	0.04
Donax variabilis	11.14	10.52	0.90	0.48	−1.00	0.32
Mytilus edulis spat	249.35	182.13	0.18	0.06	−1.37	0.18
Insect larvae	1.97	1.28	0.46	0.27	−1.16	0.25
Polychaetes	39.40	11.18	31.20	11.24	−0.55	0.58
Total prey items[b]	1,275.40	275.19	759.80	174.60	−1.58	0.12
Crab egg proportion[c]	0.27	0.05	0.27	0.05	0.06	0.95
Potential disturbance[d]	0.87	0.20	1.19	0.40	0.73	0.47
Laughing gulls <50 m	15.00	4.48	6.10	4.23	−1.47	0.14

[a] Satterthwaite *t*-test for unequal sample variance.
[b] Number of total prey is the sum of the total number of crab eggs, *Donax variabilis*, *Mytilus edulis* spat, insect larvae, and Polychaetes as well as the numbers of worms <1 cm, worm tube fragments, crustaceans, worm fragments, and snails.
[c] Crab egg proportion is the proportion of total prey items that are horseshoe crab eggs.
[d] Potential disturbance is the sum of the number of people and dogs within 200 m of the sample location.

Table 3. Top 4 candidate models with parameter estimates plus the global model and null model in AIC_c[a] model selection procedure used to best fit the dependent variable, probability of red knot presence, on all Delaware Bay beach locations and random points in May and June 2004.

Model	K	AIC_c	ΔAIC_c	w_i[b]	Coefficient	SE	Cumulative AIC_c w[c]
Model 1	7	138.75	0	0.29			
Intercept					−0.4133	0.2528	
Crab eggs					0.00327	0.0013	0.99
Mytilus spat					−0.0175	0.0550	0.94
Donax variabilis					0.3830	0.1973	0.95
Mytilus spat × crab eggs					0.000916	0.0012	0.85
Donax × crab eggs					−0.00488	0.0020	0.87
Model 2	8	139.95	1.2	0.16			
Intercept					−0.4967	0.2692	
Crab eggs					0.00331	0.0014	0.99
Mytilus spat					−0.0162	0.0323	0.94
Donax variabilis					0.3776	0.2071	0.95
Mytilus spat × crab eggs					0.000845	0.0012	0.85
Donax × crab eggs					−0.00483	0.0021	0.87
No. laughing gulls					0.00951	0.0098	0.38
Model 3	8	140.34	1.59	0.13			
Intercept					−0.3367	0.2676	
Crab eggs					0.00325	0.0013	0.99
Mytilus spat					−0.0181	0.0508	0.94
Donax variabilis					0.3988	0.1978	0.95
Mytilus spat × crab eggs					0.000943	0.0013	0.85
Donax × crab eggs					−0.00494	0.0020	0.87
No. potential disturbances					−0.0825	0.0979	0.38
Model 4	8	140.75	1.99	0.11			
Intercept					−0.4296	0.2536	
Crab eggs					0.00345	0.0013	0.99
Mytilus spat					−0.0831	0.0797	0.94
Donax variabilis					0.3434	0.1844	0.95
Mytilus spat × crab eggs					0.000763	0.0007	0.85
Donax × crab eggs					−0.00510	0.0020	0.87
Mytilus spat × *Donax*					0.2049	0.1980	0.17
Global model (all variables and interactions, see Table 2)	18	153.41	14.70	0.001			
Null model (intercept only)	2	147.59	8.84	0.004			

[a] AIC_c is Akaike's Information Criterion with small sample bias adjustment (Burnham and Anderson 1998).
[b] AIC_c weight is the percentage of total weight from all 40 candidate models that can be attributed to the specific model.
[c] Cumulative AIC_c weight of a variable equals the percentage of weight attributable to models containing that particular variable and is calculated by summing the AIC_c model weights of every model containing that variable.

Table 4. Logistic regression model predictions compared between sandy beach samples of radiotagged red knots, randomly located nontagged knots, and random points in Delaware Bay region, USA, May to June 2004.[a]

Mean P	Model 1	Model 2	Model 3	Model 4
Radiotagged knot	0.59	0.59	0.59	0.65
Nontagged knot	0.53	0.60	0.58	0.64
Random point without knots	0.44	0.39	0.43	0.43

[a] $n = 51$ radiotagged red knots from which the model was fitted, $n = 24$ nontagged, randomly located red knots, and $n = 54$ random points with no red knots. We compared the mean predicted probabilities (P) for each sample generated by each of the 4 selected models. Model 1: radiotagged vs. nontagged knot, $t = 1.08$, df $= 76$, $P = 0.29$; random point without knots vs. nontagged knot, $t = -2.69$, df $= 73$, $P = 0.01$. Model 2: radiotagged vs. nontagged knot, $t = -0.12$, df $= 67$, $P = 0.90$; random point without knots vs. nontagged knot, $t = -3.88$, df $= 64$, $P < 0.01$. Model 3: radiotagged vs. nontagged knot, $t = 0.19$, df $= 67$, $P = 0.85$; random point without knots vs. nontagged knot, $t = -3.42$, df $= 64$, $P < 0.01$. Model 4: radiotagged vs. nontagged knot, $t = 0.66$, df $= 76$, $P = 0.51$; random point without knots vs. nontagged knot, $t = -3.06$, df $= 73$, $P < 0.01$.

were to decrease substantially in this habitat during the peak of bird migration, it appears that red knots would have minimal alternative food on these beaches. Given that horseshoe crab eggs are a key resource for red knots on Delaware Bay, the finding that only 20% of beaches in the system had enough eggs to have >50% chance of finding red knot is cause for concern. Because a large proportion of the *rufa* subspecies of red knot relies on the Delaware Bay to gain fat needed to complete the migration to the arctic breeding grounds (Baker et al. 2004), we recommend precautionary management that will result in a sustained yield of horseshoe crab eggs and other food. Moreover, management should aim at minimizing disturbance of red knots and maximizing access to supplemental food resources, especially *D. variabilis* and *M. edulis* spat, for early arriving shorebirds and for use in times of low egg availability.

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Table 5. Predicted crab egg densities for varying probabilities of red knot presence[a] and the proportion of random point samples containing such egg densities ($n = 54$) from Delaware Bay sandy beaches, USA, May to June 2004.

P (red knots)	Crab eggs/m² needed[b]	Proportion of random point samples with crab eggs/m² $\geq$ needed amount
0.50	20,873	0.20
0.60	41,098	0.12
0.70	63,664	0.06
0.80	90,885	0.02
0.90	131,841	0
0.99	252,942	0

[a] We calculated the number of crab eggs per square meter needed in the top 5 cm of substrate for varying probabilities of red knot presence from the solution of the fitted logistic regression model setting all other prey types, disturbance, and gulls equal to zero. We used Model 1 from this study given it has the least number of variables and the crab egg coefficients were stable across the 4 selected models: $P(y = 1) = 1/\{1 + \exp[-(-0.4133 + 0.00327 \times \text{no. crab eggs} - 0.0175 \times \text{no. } Mytilus \text{ spat} + 0.383 \times \text{no. } Donax + 0.000916 \times \text{no. } Mytilus \text{ spat} \times \text{no. crab eggs} - 0.00488 \times \text{no. } Donax \times \text{no. crab eggs})]\}$.

[b] Other prey absent.

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